

THE BIOLOGY OF *TRICHADENOTECNUM ALEXANDERAE* SOMMERMAN (PSOCOPTERA: PSOCIDAE): I. HABITAT, LIFE STAGES AND EVENTS¹

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ABSTRACT: Populations of *Trichadenotecnum alexandrae* Sommerman are localized within apparently suitable habitat. Only 1 egg is laid during an ovipositional event. Eggs are encrusted with the contents of the gut mixed with debris collected by tapping the terminalia on the substrate. This mixture camouflages an egg once it is laid. Only a few silk strands are deposited on each egg. Eclosion and ecdysis are similar to other psocomorph Psocoptera. There are 6 nymphal stages.

Sommerman (1948) described both sexes of *Trichadenotecnum alexandrae* from North Plainfield, New Jersey, where 302 males and 425 females were collected on 27 and 29 July, 1 August, and 28 September 1947. Of all the collections she examined from other localities (Connecticut, District of Columbia, Illinois, Maine, Maryland, Massachusetts, New Jersey, New York, North Carolina, and Pennsylvania), only one from Union, New Jersey, collected on 4 June 1937, contained males, and in fact consisted of males only.

Field and laboratory investigations over a 3 year period convinced me that a complex of 4 sibling species is involved: *T. alexandrae* which is biparental (=euphrasic), but in the laboratory was found to be capable of facultative parthenogenesis (thelytoky) for only 1 generation, and 3 obligatorily parthenogenetic species, *T. castum*, *T. merum*, and *T. innuptum*, which I have described (Betz 1983a). These species occur sympatrically.

The habitat of *T. alexandrae* and also aspects of its life history observed in laboratory cultures are discussed in this paper, which is part of a series (cf. Betz 1983b, c, d) reporting these investigations.

PROCEDURE

Field and laboratory observations (and cultures) were made in 1977-9 from Illinois populations located at Moraine View State Park, McLean County (hereafter called Lake Dawson); along the Sangamon River at Lake of the Woods, Champaign County; and along the Salt Fork River at Champaign County Forest Preserve District — Homer Lake (hereafter

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called Salt Fork).

Several breeding pairs were used to start each culture and their identity was verified morphologically. The parent females were mated in the laboratory to assure the identity of the offspring. The bark used in the cultures came from the vicinity of the parent population and the bark was examined for eggs prior to use.

The cultures were kept in cotton-stoppered test tubes, supplied *ad libitum* with food (pleurococcine algae on bark), and were kept over a saturated potassium chloride (KCl) solution in closed, glass desiccator jars to maintain a relative humidity of $80 \pm 5\%$. The temperature regimen for rearing was $23.3^\circ\text{--}18.0^\circ\text{C}$ light: dark, the photoperiod was 15h: 9h light: dark, and illumination was 4300 lumens/m².

RESULTS AND DISCUSSIONS

Habitat. Most populations are found in rather open forest where the relative humidity is high and pleurococcine algae occur on the substrate (usually tree trunks). But for some unknown reason the populations at the study areas, and at the other 11 localities where I have collected this species (Illinois, Indiana, Kentucky, Maryland, Michigan, New Hampshire, New Jersey, Ohio, and West Virginia), occur in limited patches in larger areas of what appears to be equally suitable substrate. This may be related to differences in food distribution (Broadhead and Wapshere 1966, New 1970), in microhabitat, or the comparative stability of bark over a foliage habitat, making dispersal relatively unimportant (New 1969). Because pleurococcine algae are plants and are consumed by this species, it is probably safe to say that there is a host plant association involved. Statements to the contrary made about other bark-dwelling species (New 1970) were at least partly in reference to "macro" substrate, i.e., conifers, broadleaved trees, etc.

Migration to nearby tree trunks offering favorable habitat apparently occurs infrequently, even though this is a macropterous species. Similar behavior has been reported in *Cuneopalpus cyanops* (Rostock) by New (1968). Most species of bark-dwelling psocids do not fly readily (New 1969, 1971, personal observation) and generally are lacking in collections of airborne Psocoptera (Thornton 1964, Thornton and Harrell 1965, New 1969, 1975). Individuals of *T. alexanderae* in cultures becoming overcrowded or depleted of their food supply show neither a noticeable increase in activity nor a greater tendency toward flight, quite unlike some species in other families (cf. Sommerman 1943b, Mockford 1962, Turner 1974). Even movement on a tree trunk may be limited. On two occasions (at Lake Dawson and Salt Fork on 18 June and 27 July 1978, respectively) when I collected about 15 adults, their proximity in the aspirator led to a mating.

Hence, the patchy population distribution pattern probably is not due to an aggregating response by the individuals (cf. Mockford 1957, Heilbronn 1975).

Oviposition. Oviposition by 7 females from the study areas (6 mated, 1 not) was observed to be about the same. About 30-45 minutes before an egg was deposited, a female repeatedly pressed the tip of her abdomen to the substrate or probed at random for about 30 seconds, with an interval of a few seconds to 5 minutes between probes. One female dragged the tip of her abdomen along the substrate about 3 mm several times. While probing, algae and debris adhered to the ventral surfaces of a female's terminalia. When probing ceased, her abdomen returned to the normal resting position. An egg usually would be laid where her terminalia had last touched the substrate.

A female normally remained motionless about 2-3 minutes before oviposition, except for pulsing and spasmodic abdominal contractions of a few seconds duration, at about half-minute intervals. One female rubbed her hind femora along the sides of her abdomen after an abdomen spasm, possibly moving an egg into position for extrusion.

Next, an opaque, dark fluid was discharged on her terminalia and was manipulated rapidly between the epiproct, paraprocts, and valvulae for about 3-5 seconds. Then with one spasm, about one-third of an egg appeared, coated by dark fluid. About 5 seconds later another spasm exposed another third of the egg. Both egg and dark fluid were supported by the dorsal surface of the egg guide of her subgenital plate, an immobile, bracket-like structure.

Once an egg was about two-thirds exposed, it also was manipulated rapidly for about 3-5 seconds. Then she quickly pressed the tip of her abdomen down on the substrate, thereby elevating the anterior part of her body and causing here forewings to part slightly. A female paused for less than 1 second in this position, then vibrated her body from side to side. Before a female withdrew her abdomen, she slightly flexed her terminalia and dragged the tip of her abdomen about 1 mm, thus not disturbing the placement of an egg on the substrate. Depositing an egg on the substrate required about 3-5 seconds. Absorption of the dark fluid by the bark appeared to solidify an encrustation. This ovipositional behavior resembles that of *Peripsocus quadrifasciatus* (Harris) (cf. Eertmoed 1966) because an egg emerges before a female's abdomen is applied to the substrate, rather than vice versa as with *Caecilius manteri* (cf. Sommerman 1943a).

The dark fluid of an encrustation originates in the gut, as proposed by Pearman (1928a). The composition of fluid and feces are similar in *T. alexandrae*, both containing algae and debris, and thus appear to differ only in their degree of hydration. Females of *T. alexandrae* in the stage of

oviposition produce fewer feces than males of the same age, so their use in encrustations may explain this.

After a female withdrew her abdomen, she fastened several strands of silk from her labium to the egg and the surrounding substrate. She normally circumscribed the egg with silk in a roughly stellate pattern and then walked partially around it. Depositing silk took about 5-10 seconds. Each egg had about the same amount of silk whether or not eggs were present nearby. Once silk was laid down, oviposition was complete and a female walked about 5-10 mm and usually began feeding. Silk strands can keep an egg on the bark should its encrustation become dislodged.

Silk strands are produced by females that have just oviposited, by those which have yet to oviposit, and by nymphs (presumably female). Adult males do not produce silk. Females in the stage of oviposition, but not actually ovipositing, were not seen to produce silk.

Only one egg is laid during an ovipositional event. For another to be laid, the entire procedure must be repeated. Eggs are sometimes laid next to others previously laid, and cultures with a great number of eggs sometimes have clusters of two or three eggs produced in this way, giving the false impression that the eggs were deposited in succession.

Appearance of Eggs. Eggs of *T. alexandrae* are ovoid in shape and are laid with their longitudinal axes parallel to the substrate. For the first few days after oviposition, the chorion is iridescent with a grayish-white background, but later the eggs become a lusterless yellow.

Most eggs are covered completely by a hardened secretion, encrusted with algae and debris, which camouflages them on the bark. The encrustation is shaped during oviposition by the ventral surface of the epiproct and the medial surfaces of the paraprocts. Figure 1 depicts the appearance and size of a normally-shaped egg encrustation. If less dark fluid is produced during an oviposition, the egg is encrusted but the encrustation is not shaped. Some eggs are naked because they are laid without any fluid. The amount of encrusted material around an egg does not seem to affect the amount of silk subsequently attached to it.

In two separate ovipositions, the female probed with her abdomen in an area on the bark, then moved or was chased away to a differently-colored substrate on which an egg was laid. The color of these encrustations did not match their substrates. The bark debris that had been collected on the terminalia at the intended ovipositional site must have become mixed with the encrusting fluid when this was discharged, thereby causing a mismatch between the encrustation and the substrate of the actual site.

The site for oviposition apparently is selected before a female stops moving, probably because any further movement may cause a mismatch between the debris on her terminalia and the substrate, minimizing the

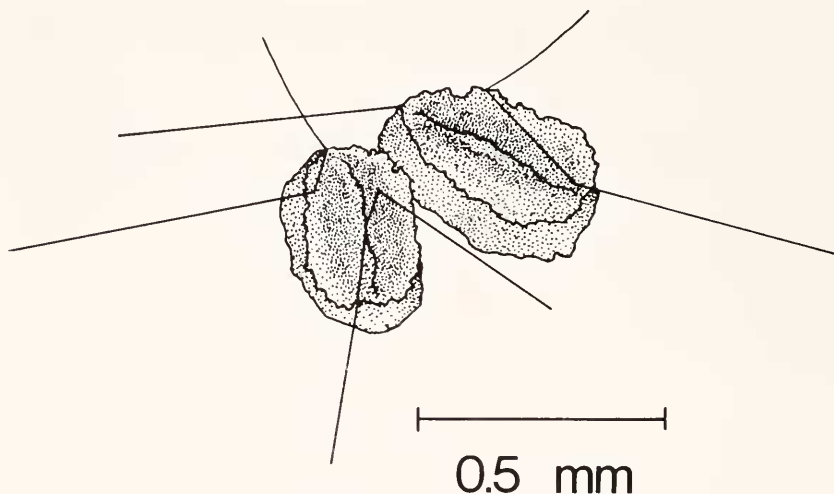


Figure 1. Encrusted eggs of *Trichadenotecnum alexanderae* with silk strands (Salt Fork culture).

effectiveness of the camouflaging encrustation. Also, further movement may result in the selection of a site ill-suited in some other way for oviposition.

Eclosion. Eclosion is similar to that of other species of psocomorph Psocoptera (cf. Pearman 1928b, Sommerman 1943a, b, c, 1944, Mockford 1957, Eertomoed 1966, Dunham 1972, Garcis Aldrete 1973). The hatching described is that of an egg from Lake of the Woods culture.

Hatching began as the top of the egg opened flapwise at its anterior end and was forced up by the head of the upright pronymph. The head emerged first, and while the pronymph had its ventral surface facing the substrate it underwent ecdysis. As molting proceeded, the nymph remained almost perpendicular to the substrate, its legs being freed before its antennae. The nymph then arched posteriorly, slowly freeing its antennae. The legs moved slightly when freed, but more actively once the antennae were freed. The nymph then fell forward, and when its legs contacted the egg it slowly crawled ahead. Emergence was completed in about 20 minutes. The nymph was cream-colored with dark purple ommatidia.

All pronymphal exuviae are grayish-white and are left about halfway out of an egg. Hatched but undisturbed eggs ($N=136$) retain the hatching flap and pronymphal exuviae.

Nymphal stages. Exuviae from 10 isolated individuals from Lake of

the Woods culture indicated there are 6 nymphal stages, and all except the first resemble adults in overall coloration. Fecal material and debris passively accumulate on nymphs of all ages, presumably because of a secretion by glandular hairs, causing most older nymphs to become camouflaged on the bark.

Ecdysis. Ecdysis is the same as that described for other species of psocomorph Psocoptera (Pearman 1928b, Sommerman 1943a, b, c, 1944, Eertmoed 1966, Dunham 1972). The following is a description of a molt from last stage nymph to adult female from Salt Fork culture.

The first sign that the nymph was about to molt was its walking with stiff appendages. It then stopped moving, about 1 minute later its antennae began to pulse at about 2 beats per second. About 20 seconds after its antennae began to beat, a pulse began in synchrony, extending from the top of the frons to the bottom of the clypeus. Then the posterior portion of its abdomen began to pulse about once every 5 seconds and the size of the nymph increased.

The dorsum of the nymph's thorax gradually split open medially and the adult emerged through this lengthening split. Excluding appendages, the thorax, head, and then abdomen emerged. The anterior end of the adult's abdomen began to withdraw from the nymphal cuticle once its head began to emerge.

Once the thorax of the adult emerged from the old cuticle, the appendages were freed in the following order: mouthparts, wings, forelegs, midlegs, hindlegs, antennae. A foreleg pulled an antenna out of the old cuticle. When an appendage was freed it quivered for about 15 seconds.

Once the appendages were out the adult was held to the old cuticle only at the posterior end of its abdomen, and was almost perpendicular to the substrate. The abdomen was freed when the adult dropped forward and crawled ahead. Once emerged, the epiproct was flexed ventrally and the paraprocts and valvulae were flexed medially in spasms for about 15 seconds.

The molt was completed in about 7.5 minutes, from the moment the nymph stopped moving to the time the abdomen of the adult became detached from the nymphal exuviae.

Directly after molting the adult was unable to stand, but could move on its coxae. The wings were curled away from the body and the forewings were pale yellow, and it took about 12 hours for the shape and color pattern to mature.

Neither nymphs nor adults of *T. alexanderae* eat their exuviae, as some psocid species do that are mycophagous or lichenophagous (cf. Sommerman 1943b, c, 1944, Mockford 1957).

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